ON THE LIMITS OF FOREST ECOSYSTEMS: DO THEY HAVE SKINS?

by
Dr. Roelof A.A. Oldeman
Professor of Silviculture, Wageningen University (NL)

RESUME

Oxf.:182

Pour individualiser un système, il faut trouver ses limites. Les limites des organismes s'appelent leurs peaux. Les systèmes vivants que sont les écosystèmes forestiers, ont-ils des peaux? Une peau est une couche filtrant les entrées et sorties d'énergie et de matière entre le système vivant et son milieu. Cela se manifeste par des gradients abruptes. Les figures 1 et 2 montrent que de tels gradients caractérisent les bordures horizontales et verticales des forêts. On peut les utiliser pour individualiser des sous-systèmes forestiers, les éco-unités. A l'intérieur de cette peau écologique, les organismes opérationalisent des boucles de feedback, menant à des processus de décision sur l'adjustement du comportement du système entier vis-à-vis des impacts exogènes. Ce modèle falsifie les théories bionomiques de Boyce (1978), ce qui signifie probablement que ni l'un ni l'autre de ces modèles représente la vérité absolue sur la forêt, les deux étant logiquement cohérents.

Introduction

This text adresses a theoretical and practical problem. The limits of physical systems are chosen by physicists (Hendekovic, pers. comm., 1985). This approach has been followed in ecology, as exemplified by the definition of an ecosystem in the Penguin Dictionary of Biology (Abercrombie et al., 1977, p. 93). The examples cited there, "a pond, a forest" show that empirical limits are used between the inside and the outside of the system. In the biology of organisms, such limits have since long been percieved as an epidermis, a membrane, a skin. This is the base of all "natural classifications", persisting implicitly in their most refined forms (e.g. Cusset, 1982).

The empirical forest limit is the place where one enters a forest. Inside a forested area, no more limits are easily perceived. The sheer welter of plants and animals may seem quite unorderly. People hence draw their own ordering limits in the ecosystems: borders of fields, forest stands or settlements. Now such man-made ecosystems would not work, i.e. their component organisms would die, unless they had something in common with the natural environment and its inner subdivisions. Hence the comparison between such systems and their limits is important both to improve our understanding and our silvicultural design.

Systems and limits

Very simply, any set of components in interaction forms a system. Both components and environment of the system are black boxes: we do not care whether they are systems in themselves or not. The situation is simplified by isolating the system from its environment, so that there are neither inputs nor outputs. With simple components, this is the set-up of physical experiments in closed vessels. Their conclusion is that no system can sustain itself. Entropy becomes maximized according to the Second Principle of Thermodynamics, and the system becomes a non-system, uninformed and chaotic.

If we peel off the isolation completely, the system becomes perfectly open. There are three levels: the environment (black box), the system, and its components (black boxes). Inputs from the environment are undifferentiated. Some increase chaos, others order in the interaction between components. Outputs are also partly chaotic, partly ordered. Inputs and outputs will balance out, and the system ceases to be individualized by any particular kind of functioning.

Closed and open systems both need to be considered according to their life-span. If infinitely short, the system would be open with infinitely fast interior processes. If infinitely long, the system would show infinitely slow prosesses and be closed. These extremes are mere reference points for forest research, concerning ecosystems open to some degree and having life-spans of intermediate duration. These are often longer than human life-spans, but always shorter than astronomical ones. Horn (1975) finds successional forest processes too slow to observe directly, and Susmel (1979) gives life-spans of 300 to 600 years for the tree components of Fagus-Abies-Picea forests in Italy.

Living systems and skins

Empirically, living systems belong to those that accumulate information inside their limits. Nature and quantity of this information are still under discussion (e.g. Asimov, 1962; Koestler, 1967; Monod, 1970; Jacob, 1970; or Sagan, 1977 are among the easier texts). Except Koestler, these authors base their arguments on the study of organisms and their subsystems: genes, nuclei, cells, organs. These can all be seen, i.e. their limits can be observed or made visible, optically or electronically.

These limits all act as filters. Nuclear membranes, cell walls or epidermes select and admit or exclude inputs and outputs. Inputs favour organisation in the system (energy, nutrients) and outputs consist of a high amount of entropy (heat, often) and a small amount of organised signals. The selectively filtering boundary layer around these systems hence allows them to accumulate information.

If we can prove this to be the case for forest ecosystem boundaries, the third bionomic theory of Boyce (1978, p. 16) can be falsified: "The theory for flows of energy and materials is falsified by discovery of centralized communication channels, sensors and decision mechanisms in the community that permit the community as a whole to regulate inflow, internal status, and outflow of energy and materials to achieve organizational goals for the forest community". This automatically would cast doubt on Boyce's first two bionomic theories, which are the basis for the third one.

The concept of a skin is not altogether new in forest ecology. Mangenot (1973) and later French authors used the name "scar vegetation" ("végétation cicatricielle") for secondary vegetation. However, they conceived the vegetation as the skin of the landscape which, when wounded, forms scars. The following paragraphs concern other scales than landscapes.

Nature and thickness of skins

Skins, e.g. our own, regulate inputs of heat, light, water and chemical substances as well as outputs. Many insecticides are substances that cheat such filtering skins. Skins have thickness, if it is only a fraction of a millimeter. Over this distance, variable factors change from their outside values to values inside the living systems. Hence there is a set of steep gradients, and at least some of those are steeper in an ant's skin than in an elephant's. Classical forest types are defined according to sites, i.e. limited by soil and water gradients. These often occur over larger distances. Such forest types hence can be considered as being thick-skinned.

Skins in organisms or cells are organically grown. But the boundaries of forest types are pedological or hydrological, that is abiotic. Often, abiotic skins cannot be directly seen, but have to be localised by measuring and surveying. The diagnosis by means of indicator species is frequently used as a short-cut to avoid this time-consuming measuring work on soil and water.

A skin is not homogeneous over its entire surface. Human outer skins differ greatly from the internal one, that covers intestines or lungs. Insect skins show supple and hard parts. Boundaries around a forested watershed also are heterogeneous. Part of their skin lies below the ground, and draws an undeep limit in the earth, surrounding the forest. The horizontal subterranean skin is invisible, and maybe coincides with the underside of the rhizosphere. Oldeman (1980) called this part the "root floor". The skin part enclosing the forest above the ground may be visualised as the forest edge and the crown canopy.

Ins and outs of forest ecosystems

The main problem here is the filtering function of the skin, the gradient question. It will be tackled by examining the above-ground part of forest ecosystems. Too little is known about their subterranean parts. The~~y~~ key notion is the differentiation between in and out, the microclimate and the macroclimate.

Let us construct an abstract, geometrical plane containing all those points on vertical climatic gradients being the last points before these gradients change shape. This plane separates one kind of physico-chemical regulation from another kind. It may be imagined as an ultra-thin transparent plastic sheet, such as used to pack food. Just under this plane, which can be constructed by gradient measuring (e.g. Cachan & Duval, 1963; Kira, 1978; also fig. 1), at least the humidity and temperature gradients show a steep change of direction. This very steepness resembles the filtering effects in organismic skins. Indeed, a rather thin layer of green leaves intercepts light, transpires and scatters the wind.

Some distance below the canopy plane, gradients loose steepness and tend towards more steady values. A second geometrical plane can be constructed with those points where the slowdown begins or reaches a certain value. Functionally, the filtering skin lies between the two planes, coinciding with the leaf canopy. The properties of this skin determine to a large extent the organisation of the forest below, as shown for instance for aerodynamic canopy roughness (Brünig, 1984). Lower leaved canopies inside the forest may cause an analogous steepening of gradients and act as "inner skins" leading to functional layering (fig. 1).

At the forest edge, the same effects occur in horizontal gradients measured at various levels (e.g. Florence, 1981). Figure 2 shows some of these steep gradients in a European forest edge, according to Jeník (1979). It also shows that along a South-North section one finds different properties in the skin at each side, just as in organisms the skin is not homogeneous.

Considering these facts, the leaf layer at the edge and the canopy of a forest may be considered as a functional skin. The skins of organisms often are built by cells. The aerial forest skin is built by tree crowns. The forest ecosystem has no epidermis and hence shows a rougher, more heterogeneous and less compact structure than plant and animal skins. It therefore can be localised more precisely by gradient measuring than by direct observation. This also is the case below the ground. Measuring is the most precise way to find root floors. Soil profiles suggest that the subterranean skin might be rough, even tentacular, and that functional root layers may exist. These hypotheses can be tested in principle in the same way as those above the ground, even if the measured factors are different.

Size and volume of forest ecosystems

For a rougher analysis, analytical scale-drawings can be used, such as profile diagrams and maps. On these, forest skins can be approximately localised. The method is faster than ecological measuring and also

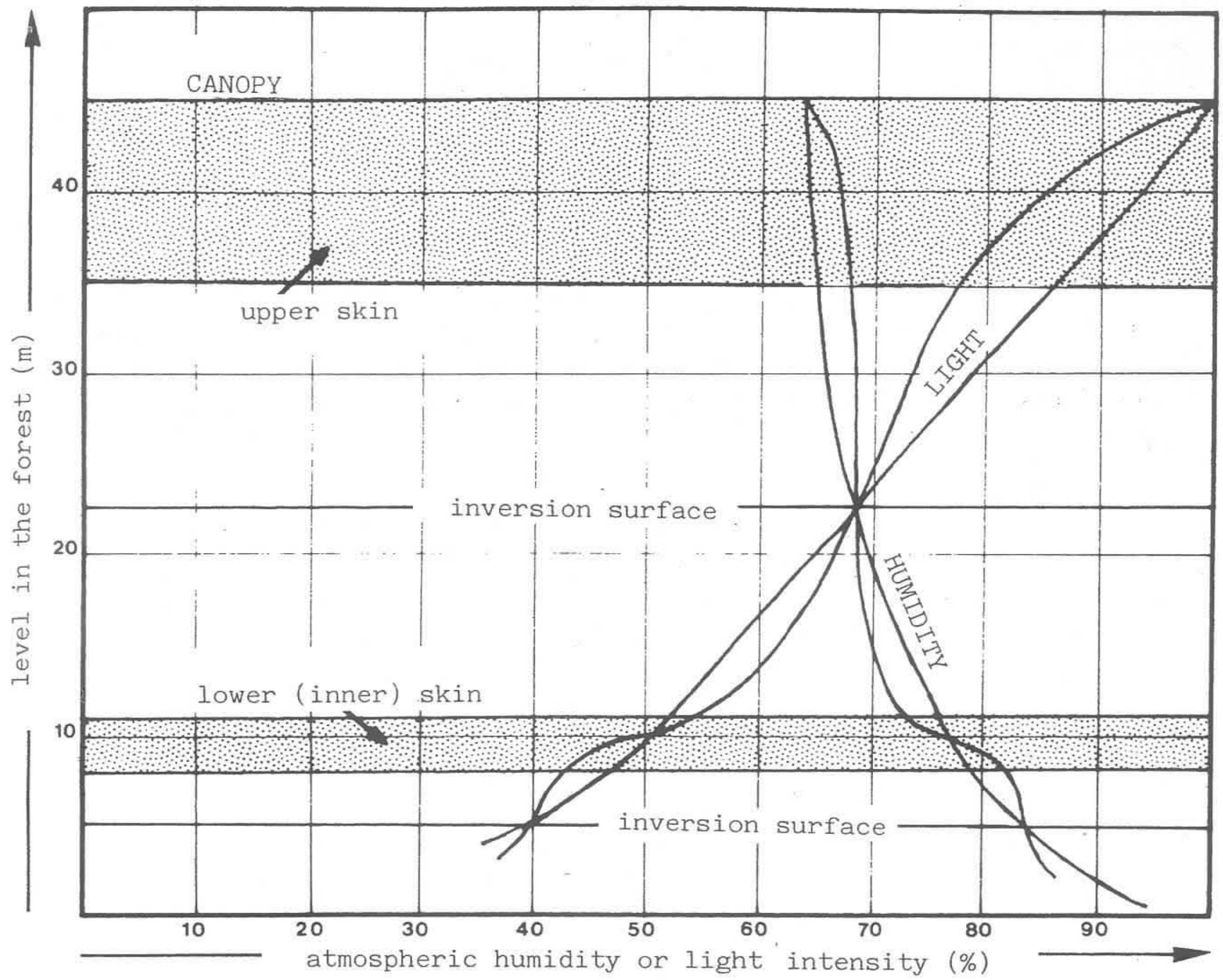

Figure 1. Horizontal forest skins in well-structured tropical forest eco-units. Schematic representation of relative light extinction and relative increase in the humidity of the air from canopy to soil, according to data from Ivory Coast and French Guayana in forests with analogous height and structure. Real extinction and humidity oscillate along mean values. Those real, oscillating gradients define skin zones where they change more abruptly (steepness to y-coordinate). On profile diagrams, these skin zones can be observed because they are linked to particular tree architectures, the trees between them being different. After Oldeman (1974).

Figure 1. Peaux forestières horizontales en forêt tropicale humide bien structurée; données de la Côte d'Ivoire et de la Guyane. Les gradients d'humidité et de lumière, entre la voûte et le sol, oscillent autour d'une ligne moyenne. Les zones de changement abrupte peuvent être conçues comme des peaux à fonction filtrante pour les entrées et sorties d'énergie et de matière. Sur des profils forestiers, elles se reconnaissent par l'architecture arborescente. D'après Oldeman (1974).

differs in that it gives no mean values over large areas, but graphically represents the spatial heterogeneity of forest skins. The first consistent heterogeneity pattern that strikes one on long profile diagrams is due to forest regeneration. Figure 3 schematically shows some different pole phases that occur frequently. The notion of forest skin can also be applied to these regeneration units.

Canopies of mature forest units differ from those of the pole phases that they surround. Between units of different ages there are edge effects (cf. also figs. 1 and 2). These vertical limits can be considered as forest skins within a forested area. The whole forest is thus subdivided in smaller systems, sub-systems or component systems. The most decisive skin parts, limiting these subsystems, are the vertical ones because they allow us to delimit the component surfaces of the regeneration mosaic, called eco-units by Oldeman (1983a). The horizontal skins of these units differ according to their developmental stage, their size and their form (cf. Oldeman, 1983b).

Figure 3 also shows that generally the skin is thicker in smaller eco-units. A forest mosaic with tree-by-tree regeneration shows almost nothing but steep horizontal gradients interacting with the vertical ones. Eco-units blend one into the other and lose their clarity. It is then easier to conceive this welter of gradients as the cause for specific interactions within a larger system, i.e. the mosaic in its skin. This larger system can be treated as one "mixed forest", a classical model, instead of a mosaic of eco-units. Both approximations make sense, and one is not more or less true than the other.

Organisms show comparable phenomena. Analytically, the florets in Compositae are the flowers, the capitulum is the inflorescence. But for all functional purposes the inflorescence behaves as a flower. Mangenot (1973) pays attention to such "transfer of functions" when subsystems are miniaturised. If ecological eco-unit functions were transfered to the mosaic when eco-units are miniaturised, the transition from the mosaic model to the mixed stand model would be justified.

Communication and co-adjustment

Edge effects, functional strata, "Stufung", mixed stands and the stand concept in itself all are familiar notions in classical silviculture. They are brought forward here in a different form, the concepts of forest skin and eco-unit being added. Is this necessary?

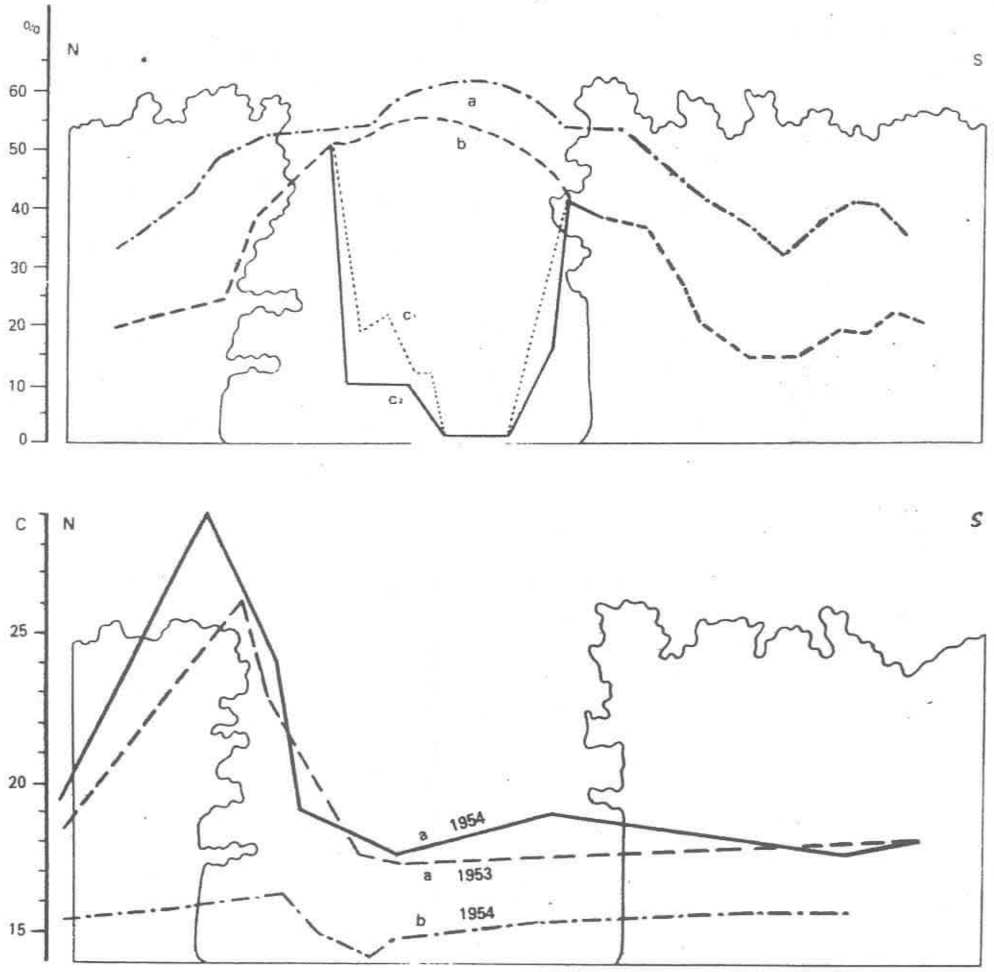

Figure 2. Vertical forest skins, shown by their "edge effects" on various gradients. North-South section through European forest gaps. Upper figure: percentage of full sunlight in broadleaved forest. a) above herb layer, before leaves appear in spring; b) same when trees are in full leaf; c1) under loose herb layer; c2) next year under dense herbs. Lower figure: Averaged integrated temperature. a) on the soil; b) 5 cm deep. Note the different properties of the north and the south skin. After Jeník, 1979.

Figure 2. Peaux forestières verticales aux bords de chablis Européens en forêt feuillue du Nord au Sud. En haut: pourcentage d'irradiation solaire. a) en dessus des herbes, arbres sans feuilles; b) même, arbres feuillus; c1) sous des herbes éparses; c2) année suivante, herbes denses. En bas: température moyenne intégrée. a) niveau du sol; b) 5 cm de profondeur. Noter propriétés différentes de la peau au Nord et au Sud. D'aprés Jeník, 1979.

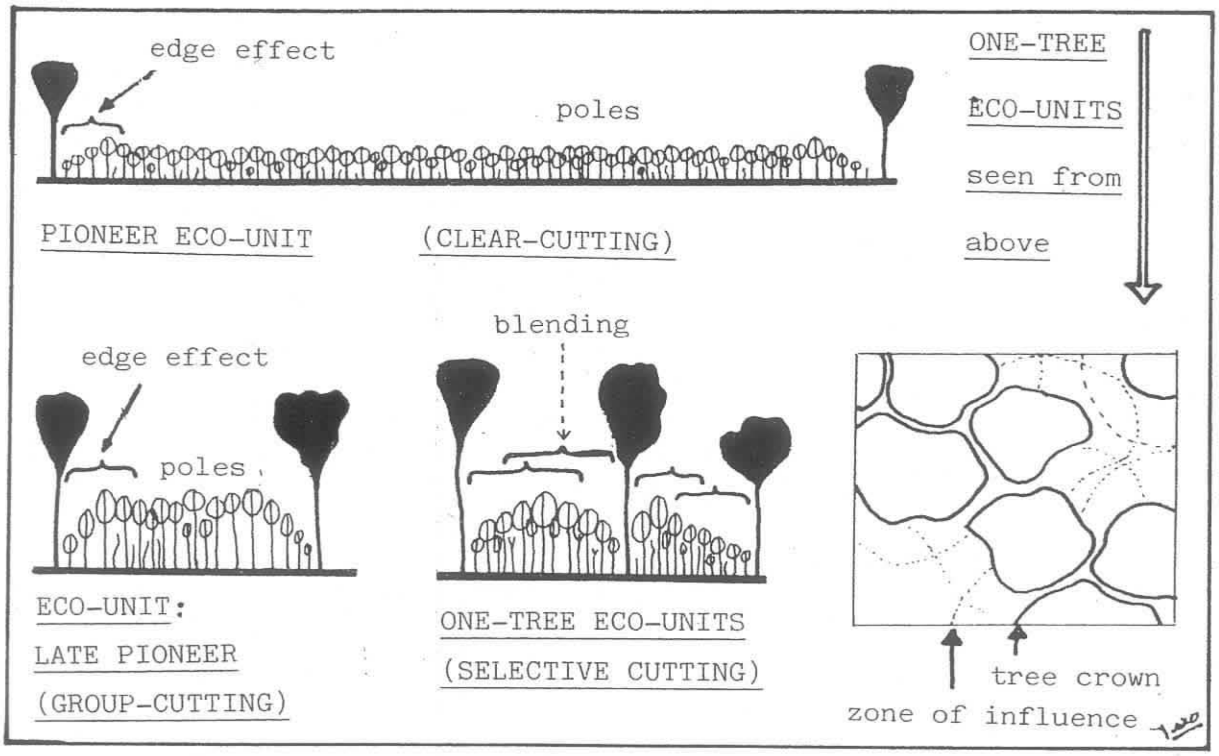

Figure 3. Frequently occurring eco-units of different sizes, all in the pole stage. Note different properties of mature tree crowns (black) and immature tree crowns (open) as components of the horizontal forest skin. Tree-by-tree regeneration leads to very small eco-units, all in interaction, blending, so that a mixed-stand model makes sense as well. After Oldeman, 1983c.

Figure 3. Eco-unités fréquentes de dimensions différentes, toutes en phase de gaulis. Notez les propriétés différentes des cimes mûres (en noir) et immatures (ouvertes) comme composantes d'une peau forestière horizontale. La régéneration arbre-par-arbre mène à des chablis petits, tous en interaction et moins faciles à distinguer: ici, un modèlle de peuplement mixte est également utile. D'après Oldeman (1983c).

The concept of skin allows to bridge the gap between the limitless and ageless ecosystem concept from most ecological studies, and the stand-and-site notions from forestry. The scientist so may better understand forests as natural systems, i.e. systems with natural limits and life-spans. And the forester thus may gain better access to the scientific notions of systems analysis.

The concept of eco-unit may help to surmount the idea that a forest is a collection of trees. Eco-units are systems built by and functioning with myriads of species, most of which are not trees. The mixed forest model gains in richness if viewed at the same time as a mosaic built by small eco-units, because each of these units contains many more organisms than just trees.

All recent research on forest ecology tends to prove, however, that the eco-unit components determining the upper and the lower skin parts are the trees. Both parts are completed by other organisms, such as epiphytes, lianes and epiphylls in the canopy, and mycorrhizal fungi in the rhizosphere. These modify the functions of both skin parts and hence codetermine the behaviour of the whole system.

The vertical skins are built by edge trees, small trees, shrubs, climbers and other plants. Vertical skins become less clear-cut when neighbouring eco-units acquire the same height, because differences between their inner climates diminish with the canopy development of the youngest one. With measuring gear and indicator species, some subtle and remnant ecological skin might still be found.

The dorsiventral architecture of eco-units has much in common with that of dorsiventral organs, such as leaves. They show an upper and a lower epidermis, built by particular components,cells or trees. The intercellular spaces look like spaces between trees. Just as an organ, the whole eco-unit system in its skin can adjust its behaviour to changing circumstances, e.g. increasing pollution.

Canopy leaves and mycorrhizal hyphae seem to be the prime sensors of exogenous impacts. Communication of signals is primarily through the sap stream in trees. Secondary signals are transmitted through the ecosystem skin, after it has reacted to primary signals. The grass on the forest floor reacts as a sensor to increased light, then as an effector on tree roots and mycorrhizal behaviour. Decisions taken this way for instance are shifts in symbiotic relationships, in litter decomposition processes or in reproductive plant and animal behaviour. Temporary stress factors lead to reversible decisions (adjustment). Stand behaviour under pollution strongly resembles its behaviour in drought. Permanent stress leads to the limits of the same behaviour and becomes lethal. The adjusting behaviour is of the ecosystem, not of the components in isolation.

Many of the component organisms in these complex feedback loops cannot survive outside certain forest eco-units of a certain architecture and age. The survival of the eco-unit is one of the "goals" of their life-strategy, necessary for their own survival. As far as this "division of loyalties" is concerned, this corresponds to the role of, e.g., cells in tissues. Both system and component have to survive.

Coevolution of organisms as subsystems of a forest ecosystem (eco-unit, mixed stand...) is a prerequisite for their continuing co-adjustment, allowing the whole system to adjust its behaviour. Eco-unit adjustment is a reaction to both structured impacts from the regeneration mosaic and stochastic impacts from climate and soil. The narrow feedback relations between forest organisms sometimes are borne by material links. Anastomosing root networks, as in Douglas fir or Okoumé stands (communication: sapstream) or interweaving of adapted mycelium in mycorrhizal roots (both sensor and effector functions) are examples.

This is no different from other living systems, elsewhere in the hierarchy. If, by knowledge of the site properties and the regionally available plant and animal species one cannot deduce the organisation and development of a forest ecosystem (Boyce, 1978), the same can be said for organisms: the organisation in space and time of an oak tree cannot be deduced from the properties of the environment and knowledge of available plant organs in Fagaceae.

Interclusion

This discussion cannot be brought to a conclusion here and now, if ever. Hence this paper ends with a modest interclusion.

Forest ecosystems have boundary layers that are functional analogs of organismic skins. These skins allow to individualise forest ecosystems at two hierarchic levels: eco-units and regeneration mosaics (stands and forest types). This model falsifies the bionomic theories of Boyce (1978): ecosystems have a survival "goal" shared and implemented by their plants and animals; biological sensors, effectors and negative feedback loops lead to behavioral decisions in whole ecosystems; and inflow, outflow and internal status of energy and matter to achieve ecosystem survival are regulated by the ecological skin. Boyce's fourth theory is not contradicted, because in its simplest form it just says that forests are living, i.e. growing systems that change with time.

This does not mean that Boyce's theories are absolutely false and the ones presented here are absolutely true. It simply implies that several logically coherent models of forest ecosystems can be conceived, each having its merits as a tool for the understanding of certain theoretical and practical problems. As long as no better, more unifying concepts are thought out, we'd better use the whole intellectual tool kit so as not to overlook essential information.

Bibliography

Abercrombie, M., Hickman, C.J., & Johnson, M.L., 1977 (6th ed.), A dictionary of biology. Harmondsworth (UK), Penguin Books Ltd, 311 pp.

Asimov, A., 1962, Life and energy. New York, Avon Publ.; Discus/Avon books W299: 378 pp.

Boyce, S.G., 1978, Theory for new directions in forest management. US Dept. of Agric., Forest Service Research Paper SE-193: 19 pp.

Brünig, E.F., 1984, Designing ecologically stable plantations. in Wiersum, K.F. (ed.), Strategies and designs for afforestation, reforestation and tree planting: 348-359. Wageningen (NL), Pudoc.

Cachan, P., & Duval, J., 1963, Variations microclimatiques verticales et saisonnières dans la forêt sempervirente de basse Côte d'Ivoire. Annales Faculté des Sciences, Dakar (Senegal): 87 pp.

Cusset, G., 1982, The conceptual bases of plant morphology. in Sattler, R. (ed.), Axioms and principles of plant construction, The Hague, Nijhoff/Junk Publ. pp. 8-86.

Florence, J., 1981, Chablis et sylvigénèse dans une forêt humide sempervirente du Gabon. Thèse de Spécialité, Université de Strasbourg.

Horn, H., 1975, Forest succession. Scientific American, 232, 5: 90-98.

Jacob, F., 1970, La logique du vivant. Paris, Gallimard: 354 pp.

Jeník, J., 1979, Pictorial encyclopedia of forests. London, Hamlyn: 495 pp.

Kira, T., 1978, Community architecture and organic matter dynamics in tropical lowland forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. in Tomlinson, P.B. & Zimmerman, M.H. (ed.) Tropical trees as living systems, chapter 24, London, Cambridge Univ. Press.

Koestler, A., 1967, The ghost in the machine. London, Pan Books Ltd., Picador edition:384 pp.

Mangenot, G., 1973, Données élémentaires sur l'Angiospermie. Abidjan

(Ivory Coast), Annales de l'Université d'Abidjan, série E, VI, vol. 1: 233 pp.

Monod, J., 1970, Le hasard et la nécessité. Paris, Ed. du Seuil: 197 pp.

Oldeman, R.A.A., 194, L'architecture de la forêt guyanaise. Paris, Mém. ORSTOM, 73: 204 pp.

Oldeman, R.A.A., 1980, Grondslagen van de bosteelt (Principles of silviculture, in Dutch, out of print). Wageningen Agric. Univ., Dept. of Silviculture: 201 pp.

Oldeman, R.A.A., 1983a, The design of ecologically sound agroforests. in Huxley, P. (ed.), Plant Research and Agroforestry, chapter 14, Nairobi (Kenya), ICRAF

Oldeman, R.A.A., 1983b, Tropical rain forest, architecture, silvigenesis and diversity.in S.L. Sutton et al. (ed.), Tropical Rain Forest: Ecology and Management: 139-150, Oxford, Blackwell Scient. Publ.

Oldeman, R.A.A., 1983c, Veldgids transecttekenen (Field guide for transect drawing ; in Dutch). Wageningen, Agric. University, Dept. Silviculture: 68 pp.

Sagan, C., 1977, The dragons of Eden. New York, Random House Inc., Ballantine Books: 271 pp.

Susmel, L., 1979, Modello strutturale di Abetine e Peccete primarie. Atti Instit. Ecologia e Selvicoltura Padova, 1,1: 48 pp.